Local extinction and colonisation in native and exotic fish in relation to changes in land use

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Abstract. Distribution patterns of many native and exotic fish species are well documented, yet little is known about the temporal dynamics of native and exotic diversity in relation to changes in land use. We hypothesised that colonisation rates would be higher for exotic fish species and that extinction rates would be higher for native species in large stream systems. We also predicted that cold-water species would be more impacted than thermally tolerant species. To test these hypotheses, we used generalised linear mixed models to compare changes in native and exotic fish species richness over 10 years in a French drainage basin subjected to landscape alterations. Exotic fish were more susceptible to local extinction than the native ones. Extinction was greater among cold-tolerant species and at higher elevations. Colonisation by exotic species was higher at lower elevations. Although a decade of expanding urbanisation affected fish colonisation, agricultural lands experienced higher extinction rates. In the context of global changes in land use and population pressure, our study suggests that the temporal dynamics of fish diversity are driven by landscape alterations as well as by the thermal tolerance of species.

Additional keywords: agriculture, freshwater fishes, introductions, thermal preferences, urbanisation.

Introduction

Worldwide, many countries have established national Biodiversity Action Plans (BAPs, e.g. USA, Australia, New Zealand, Tanzania). These policy changes were implemented in response to a growing concern that development over previous decades was having a significant impact upon biodiversity, despite considerable benefits to the citizens of nations. Under this framework, assessing the effects of landscape alterations (e.g. urbanisation, agriculture) on community dynamics is now a priority for biological conservation (McKinney 2002). Much of the current research has reported declines in the diversity of target organisms (e.g. various invertebrates, fish, mammals or plants) in relation to landscape alterations, from local to global scales. Apart from their direct effects upon diversity and ecological processes, changes in land use or habitat destruction can also promote biological invasions by exotic species. These biological invasions constitute a significant component of global environmental changes and may affect human health and wealth, ecosystem functions and native biological diversity (Vitousek *et al.* 1996). Freshwaters are particularly subjected to habitat degradation, hydrologic alterations, pollution and the spread of invasive species (Dudgeon *et al.* 2006). For example, recent estimates indicate that 25% of the world's freshwater fish are threatened with extinction (Vié *et al.* 2009).

Many species present a metapopulation structure, with colonisation/extinction occurring at local scales (Case 1991). The equilibrium between both processes determines trends in population ranges. However, research has focussed on characterising colonisation and waves of establishment (e.g. Leprieur *et al.* 2008; Gozlan *et al.* 2010) and little is known about the temporal stability of both exotic and native populations in invaded areas (Strayer *et al.* 2006). In this context of species loss and biological invasions, the response of local communities to environmental changes can be perceived in terms of colonisation by some sets of species and extinction of other species over time. Local colonisation is defined as a species being detected in a location from which it was previously absent, whereas local extinction is defined as the absence of a species in a location where it was previously present (Nichols *et al.* 1998). Assuming that exotic species colonise ecosystems as agricultural or urban land cover increases (Pool *et al.* 2010), one may predict that exotic and native species differ in their colonisation/extinction responses to environmental changes (Kopp *et al.* 2009).

Spatial patterns of native and exotic species richness have been extensively studied along gradients of disturbance (e.g. Kopp *et al.* 2009). However, little is known about the temporal dynamics of native and non-native diversity in relation to changing landscapes. Although habitat degradation, climate change or biological invasions can cause immediate extinctions, there is often a considerable lag between environmental changes and the subsequent extinctions (Olden *et al.* 2010). Most studies of the distributions of exotic species have been based on short-term surveys and have, thus, yielded snapshots that lack a temporal context (Strayer *et al.* 2006). In light of recent urban and agricultural development, short-term assessments are likely to be inadequate to describe colonisation/extinction patterns and the roles that exotic species play over time in the areas they invade. Using long-term data on species occurrence or comparing past vs present habitat characteristics may be used to address these aims (Olden *et al.* 2010).

In this study, we focussed on the Adour-Garonne stream system (France). The drainage basin of this system is subjected to urbanisation and extensive agriculture. River fish are the most frequently introduced freshwater organisms worldwide (Leprieur *et al.* 2008); therefore, they are relevant model organisms to study the contribution of native and exotic species to biodiversity patterns in a spatial and temporal context. Our specific aim was to assess the extent of changes in native and exotic fish species richness over the past decade. Assuming that increasing anthropogenic impact enhances the chances of successful invasion by exotic fishes and that exotic and native species differ in their responses to environmental changes (water temperature, urbanisation, agriculture), we hypothesised higher colonisation rates for exotic species and higher extinction rates for native ones. In the context of global warming, we also predicted that cold-water species would be more prone to extinction than thermally tolerant species. To test these hypotheses, we analysed the patterns of colonisation and extinction by native and exotic fish at 100 sites from 1994–97 to 2004–07, in relation to changes in land use, the location of sites within the stream system and the thermal preferences of species (from cold to warm waters).

Materials and methods

Study area and data collection

The Adour-Garonne stream system (south-western France) has a 116 000 km^2 drainage basin. We selected 100 sampling sites ranging from 6 to 1800 m above sea level (a.s.l., see Fig. S1, available as Supplementary Material to this paper), representing rivers from high mountain, plain and coastal areas. Samples were collected by electrofishing during low-flow periods. To avoid pseudo-absence data, each site was sampled three times between 1994 and 1997 and then three times between 2004 and 2007. The sampling reaches (~100 m long) were similar between the periods. A species with three absences during a given period was considered as absent. The biological variables assigned to each site were the colonisation by new fish species or the extinction of species from one period to the other. As fish temperature preferences have a strong influence upon species' potential range within the river continuum (Buisson *et al.* 2008), fish were divided into warm-, cool- and cold-water types with regard to their preferred thermal conditions (Magnuson *et al.* 1979). We then included the thermal tolerances of fish: cold-, cool- or warm-tolerant (according to Kottelat and Freyhof 2007) as explanatory variables in the analysis.

For each site, a geographic information system (GIS, Mapinfo Professional 7.8, Troy, NY) was used to delineate a geographical buffer zone representing a 1000-m radius centred on the site. This size falls within that of the 'reach buffer' defined by Allan (2004) as a buffer of 100 to several hundred metres in width on each bank and some hundreds of metres to a kilometre in length). In practice, the width of the buffer zone is often adapted to the landscape characteristics of the studied areas and ranges from 30 to 100 m on each side of the river (discussed by Compin and Céréghino 2007). Sampling sites were then characterised using elevation above sea level (m) and three land-cover variables intended to account for anthropogenic pressure. The three land-cover variables, described for the two periods 1994–97 and 2004–07, were percentage area within a buffer zone covered by forest (areas occupied by forest and woodlands with native or exotic coniferous or deciduous trees; scrub and herbaceous vegetation associations), urban areas (industrial, commercial and transport units; artificial and non-agricultural vegetated areas) and agricultural areas (arable lands, permanent crops and pasture). Digital land-cover information was obtained from the CORINE land-cover database for Europe (European Environment Agency, http://www.eea.europa.eu/, accessed June 2010). This database was generated from orthorectified satellite images and provides thematic GIS map layers including up to 44 land-cover classes with a mapping scale of 1 : 100 000. These four variables were chosen because they characterise the location of sampling sites within the stream system and within the regional landscape mosaic and they are easy to describe using a GIS.

Data analyses

We analysed the relationship of different ecological factors and the patterns of colonisation and extinction in 100 different sites in four different river basins. We fitted a generalised linear mixed model (GLMM) to the presence–absence data collected for each species in each different site in 1994–97 and 2004–07. Both basin and site within a basin were included as random factors to control for local non-independence of the data. We modelled the non-independence of data coming from the same species by assuming a common positive correlation between data from the same species coming from different localities and a zero correlation with the data of other fish species (see Blackburn and Duncan 2001 for a similar approach). We constructed two different models: one for local colonisations and another for local extinctions. For the model of local colonisations, we considered only the data of negative census for each species × locality in 1994–97 and used the presence/absence data for 2004–07 as the response variable modelling the probability of obtaining a positive count in 2004–07. For the extinctions model, we used the data of positive census for each species × locality in 1994–97 and again used the presence/absence data as the response variable, modelling the probability of a negative census in 2004–07.

All calculations were done with the GLIMMIX procedure in SAS 9.2. (SAS Institute, Cary, NC, USA) using a binomial

Table 1. Models analysing the patterns of fish extinction for cold-tolerant species (cold), cool-tolerant species (cool), thermally-tolerant species (warm) and for native vs. exotic species

Only variables with $P < 0.05$ are interpreted as statistically significant. Estimates correspond to slope values associated to each factor and are only reported for significant effects retained in the final model

Extinction	*F*-value	d.f.	*P*-value	Estimate ± s.e.
Elevation	6.79	1,932	0.009	0.5448 ± 0.2090
Cold	4.08	1,32	0.05	Non-cold, −0.7309 ± 0.6320; cold, 0
Cool	0.07	1,31	0.79	–
Warm	0.13	1,31	0.72	–
Native vs exotic	18.51	1,32	0.0001	Exotics, 1.2880 ± 0.2994; native, 0
Urbanisation	0.28	1,931	0.60	–
Agriculture	7.53	1,932	0.006	0.0103 ± 0.0037
Change urban land cover	0.54	1,931	0.46	–
Change agricultural land cover	0.14	1,931	0.70	–

Table 2. Models analysing the patterns of fish colonisation (for legend see Table 1)

Only variables with $P < 0.05$ are interpreted as statistically significant. Estimates correspond to slope values associated to each factor and are only reported for significant effects retained in the final model

Colonisation	*F*-value	d.f.	*P*-value	Estimate ± s.e.
Elevation	76.95	1,2692	<0.0001	−1.2457 ± 0.1420
Cold	10.07	1,34	0.003	Non-cold, 1.2534 ± 0.3894; cold, 0
Cool	0.78	1,33	0.38	–
Warm	5.02	1,34	0.02	Non-warm, 0.6912 ± 0.3085; warm, 0
Native vs exotic	0.67	1,33	0.42	–
Urbanisation	0.69	1,2691	0.41	–
Agriculture	1.03	1,2691	0.31	–
Change urban land cover	21.80	1,2692	<0.0001	0.0796 ± 0.0170
Change agricultural land cover	1.11	1,2692	0.29	–

distributed error and a logit link function. We followed a backwards selection procedure. The least significant variable was excluded from the model which was then recalculated until only explanatory variables increasing fit with a $P < 0.05$ were retained. Environmental variables were log-transformed to fit a normal distribution (elevation) or ranked when not normalised by usual transformations (% urban, % agricultural area, changes in covers of both land uses). As land use was classified in three exclusive categories (i.e. % urban, agricultural and forest areas), a strong colinearity existed between the three variables. For this reason, only two of the categories (% urban and % agricultural areas) were included in further analyses, but statistically significant relationships of the same sign for both variables must also be interpreted as a negative relationship for the third one. The category excluded from the analyses was chosen at random but qualitatively identical results emerged when excluding another of the habitat change categories. Changes in land cover were calculated as the difference in the proportion of habitat between 2004–07 and 1994–97.

Results

Thirty-seven fish species were found in the Adour-Garonne basin, among which 16 were exotics (according to Keith and Allardi 2001; for complete list see Table S1, available as Supplementary Material to this paper). Our models indicate that elevation and land-use variables could explain local extinction and colonisation patterns in river fish in this basin.

Fish extinction

The extinction model revealed that local extinction was significantly higher among cold-tolerant species ($F_{1,32} = 4.08$; $P = 0.05$; Table 1), so that the extinction rate was higher at higher elevation ($F_{1,932} = 6.79$; $P = 0.009$). Exotic species had a higher tendency to local extinction compared with the native ones ($F_{1,32} = 18.51$; $P = 0.0001$; Table 1). The intensification of agriculture (up to 46% at some of the studied sites) fostered local extinction of fish species ($F_{1,932} = 7.53$; $P = 0.006$; Table 1).

Fish colonisation

The colonisation model revealed that colonisation has been greater at low elevations ($F_{1,2792} = 76.95$; $P < 0.0001$; Table 2). Colonisation appeared to be lower for both cold- and thermally-tolerant species, either native or exotic ($F_{1,34} = 10.07$; $P = 0.003$ and $F_{1,34} = 5.02$; $P = 0.02$ respectively). Finally, the expansion of urban lands between 1994–97 and 2004–07 (up to 17%) positively affected colonisation ($F_{1,2792} = 21.8$; $P < 0.0001$; Table 2).

Discussion

In the Adour-Garonne stream system, fish colonisation was higher at low elevations. According to the 'biotic resistance hypothesis', the higher fish richness at downstream sites (Kopp *et al.* 2009) should prevent the establishment of non-native

species through competitive exclusion (Leprieur *et al.* 2008; Olden *et al.* 2010). However, because colonisation was higher in these areas, we can infer that higher species richness did not limit the capacity of exotic species to establish. Instead, the hypothesis of 'biotic acceptance' can be applicable in our system. This hypothesis predicts that the factors that support greater native richness in a region (e.g. abundant resources and habitat heterogeneity) also promote the establishment of non-native species. Therefore, biological interactions may have played a negligible role in the observed patterns, contrary to environmental factors.

Cold-tolerant species, which experienced the greatest extinction rates, are typically confined to mountain streams in the Adour-Garonne basin. According to Balcombe *et al.* (2011), these cold-water tolerant species are particularly sensitive to increased stream temperature, especially when they are located at their temperature limits (Morrongiello *et al.* 2011) because temperature has a direct physiological effect on these fish. As fish are poikilotherms, water temperature strongly controls population dynamics through metabolism, growth and fecundity (Lobon-Cervia *et al.* 1996), thus, forming a key physicochemical habitat filter (Poff 1997) that determines species' potential refuge sites along the river continuum (Murawski 1993). Mountain streams may also represent harsh environments which are physically stressful (higher river competence and erosive forces generated through the combination of slope with other variables such as water depth and current velocity and snowmelt floods). These natural environmental factors, combined with low connectivity among suitable sites in cold headwater streams, may be responsible for low levels of colonisation at high altitude sites (Gido and Brown 1999).

At the same time, the intensification of agriculture (including pasture lands in mountainous areas) may have fostered local extinction of fish species. The agricultural landscape of southwestern France and western Europe in general, has radically changed over the past decades (Meeus *et al.* 1990) as a result of land-use conversion, intensification of production systems and abandonment of traditional practices. The principal pressures causing biodiversity loss in the countryside are habitat fragmentation, degradation and destruction due to land-use change. Important sources of agriculture-derived pollution include the inflow of nutrients, pesticides and heavy metals from diffuse and point sources (Allan 2004). Fragmentation impacts the connectivity between suitable habitats (Fahrig 2003) and ultimately affects community dynamics (Denoël and Ficetola 2008).

Expansion of urban lands positively affected colonisation. Although our model does not allow us to distinguish whether expansion of urban lands favours native or exotic fish colonisation, close scrutiny of the dataset revealed that colonizers were mainly exotic species such as *Pseudorasbora parva* (topmouth gudgeon) and *Silurus glanis* (European catfish). A recent study in the United States revealed that non-native species dominate watersheds supporting high densities of dams, roads and urban and agricultural landscapes, whereas watersheds characterised by upstream land protection support fish communities with a strong complement of native species (Pool *et al.* 2010). According to Leprieur *et al.* (2008), the 'human activity hypothesis' (i.e. by disturbing natural landscapes and increasing the importation of non-native species, human activities facilitate greater levels of establishment) best explains the patterns of non-native fish richness in river basins. In our study area, landscapes characterised by increasing proportions of urban land use were successfully colonised by exotic species, thus, supporting the idea that association with humans increase the chances of successful dispersal and establishment in non-native species.

In conclusion, the colonisation and extinction patterns highlighted in this study only partially matched our *a priori* expectations. Over a decade, exotic fish were more susceptible to local extinction than the native ones. The 'three tens' rule (one imported species in 10 appears in the wild, one in 10 of these become established and one in 10 of established non-indigenous species becomes a pest) which was initially formulated for exotic plants (Williamson and Fitter 1996) probably does not apply to exotic fish, because these animals are intentionally introduced by humans in potentially suitable habitats. Therefore, it is likely that extinction in exotic fish was not related to unsuccessful settlement, but rather to external factors such as water temperature or flow variability (Costelloe *et al.* 2010).

Regardless of their biogeographic status (either native or exotic), cold-tolerant fish were more prone to extinction than the cool- or thermally tolerant ones. This may be due to the rapidity of climate changes which are predicted to exceed the ability of many species to adapt to new environmental conditions (Morrongiello *et al.* 2011; Olden *et al.* 2011). Therefore, our results support the hypotheses that: (i) all fish communities are susceptible to invasion regardless of native species richness (Moyle and Light 1996; Gido and Brown 1999); and (ii) water temperature, or its changes, is a major driver of fish extinction in human-impacted landscapes. In light of future climate scenarios, our study further suggests that mountain ranges are the areas at greatest extinction risk for poikilotherms and our ability to detect responses of native and exotic species to landscape alterations using a combination of simple environmental variables exemplifies a cost-effective technique for assessing areas at greater invasion risk in large stream systems.

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